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Altered climate leads to positive density-dependent feedbacks in a tropical wet forest

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Abstract

Climate change is predicted to result in warmer and drier Neotropical forests relative to current conditions. Negative density-dependent feedbacks, mediated by natural enemies, are key to maintaining the high diversity of tree species found in the tropics, yet we have little understanding of how projected changes in climate are likely to affect these critical controls. Over 3 years, we evaluated the effects of a natural drought and in situ experimental warming on density-dependent feedbacks on seedling demography in a wet tropical forest in Puerto Rico. In the +4°C warming treatment, we found that seedling survival increased with increasing density of the same species (conspecific). These positive density-dependent feedbacks were not associated with a decrease in aboveground natural enemy pressure. If positive density-dependent feedbacks are not transient, the diversity of tropical wet forests, which may rely on negative density dependence to drive diversity, could decline in a future warmer, drier world.

KEYWORDS
arbuscular mycorrhizal fungi, climate change, negative density dependence, positive density dependence, tropical wet forest

1 | INTRODUCTION

Tropical forests support at least 50% of the Earth's biodiversity (Wilson, 1992) and play a critical role in regulating global climate, exchanging more water and carbon dioxide with the atmosphere than any other terrestrial biome (Wright, 2010). If ecosystem functions, such as water and carbon dioxide exchange with the atmosphere, are positively correlated with ecosystem diversity, then a loss of diversity in tropical forests could have dramatic effects on global climate. Climate models predict that tropical forests will experience an increase in temperature of several degrees, as well as an increase in the frequency and severity of drought events (Karmalkar, Bradley, & Diaz, 2011; Lyra et al., 2017). However, we have little understanding of how these projected changes will affect the underlying mechanisms that support the high tree diversity found in these ecosystems. Here, we address this knowledge gap by investigating how natural drought and in situ experimental warming altered plant negative density dependence, a crucial control of tree diversity.

The prevailing theory for the high tree diversity found in tropical forests is that individuals of the same species (conspecifics) limit themselves more than they limit individuals of other species (heterospecifics). These negative density-dependent effects are mediated in part by natural enemies (e.g., soil pathogens, herbivores) that exhibit host preferences (the Janzen–Connell hypothesis; Connell, 1971; Janzen, 1970). Recently, the potential for plant mutualists to influence plant density dependence has been recognized (Bachelot, Uriarte, McGuire, Thompson, & Zimmerman, 2017; Liang et al., 2015). Specifically, interactions among plants and arbuscular mycorrhizal (AM) fungi, the most common mycorrhizal fungi in tropical forests, can alter the composition of tropical tree communities (White, 1969). In exchange for carbon, plants receive benefits from associating with AM fungi, such as increased nutrient uptake, water uptake, and plant defense (van der Heijden et al., 1998). Furthermore, AM fungi are important for maintaining high tropical tree diversity by decreasing seedling mortality (Bachelot et al., 2017; Liang et al., 2015). Overall, if climate change alters the underlying biotic controls on plant density dependence, such as the prevalence of natural enemies and AM fungi, tropical forests could experience dramatic changes in community composition, which, in turn, could affect forest structure and function.

Traditionally, plant density dependence studies have not looked at temporal variations in plant density dependence in relation to climate. However, two studies suggest that climate could play an important role in determining the strength of negative density dependence in tropical forests (Bachelot, Kobe, & Vriesendorp, 2015; Comita et al., 2014). First, in a meta-analysis of experimental seed and seedling survival studies (Comita et al., 2014), the authors found that the strength of negative density dependence significantly increased with increasing precipitation. An observational analysis of 10 years of seedling survival data from Costa Rica found strong negative density dependence in hot and wet years (Bachelot et al., 2015). However, no studies have investigated the mechanisms underlying the observed relationships between climate and density dependence. Understanding these mechanisms is challenging because several competing factors are at work, such as aboveground and belowground natural enemies, mutualists, and plant functional traits, each of which could respond to climate differently. Below, we briefly illustrate the complex ways in which climate could influence agents of negative (e.g., plant natural enemies) and positive (e.g., mutualists) density dependence.

Increased temperature could influence the strength of density-dependent feedbacks through both direct and indirect effects on natural enemy communities (van der Putten, Macel, & Visser, 2010). Temperature can directly influence natural enemy population growth rate, spread, and pathogenicity (e.g., Bale et al., 2002; Chown & Terblanche, 2006; Coley, 1998; Wolda, 1978). Additionally, temperature can indirectly influence enemy communities via its effects on plant and soil chemistry, such as nitrogen content (e.g., Coley, 1998). The direction of the effect of climate on natural enemies is highly species-specific (van der Putten et al., 2010). However, a large-scale analysis of fossil records indicated that insect richness and the rate of herbivory increased during the warm Eocene compared to the cool Paleocene (Wilf & Labandeira, 1999). Therefore, warming might be associated with an increase in the richness of natural enemies and increased herbivory, resulting in strong negative density-dependent growth and survival (Figure 1a,c). There is

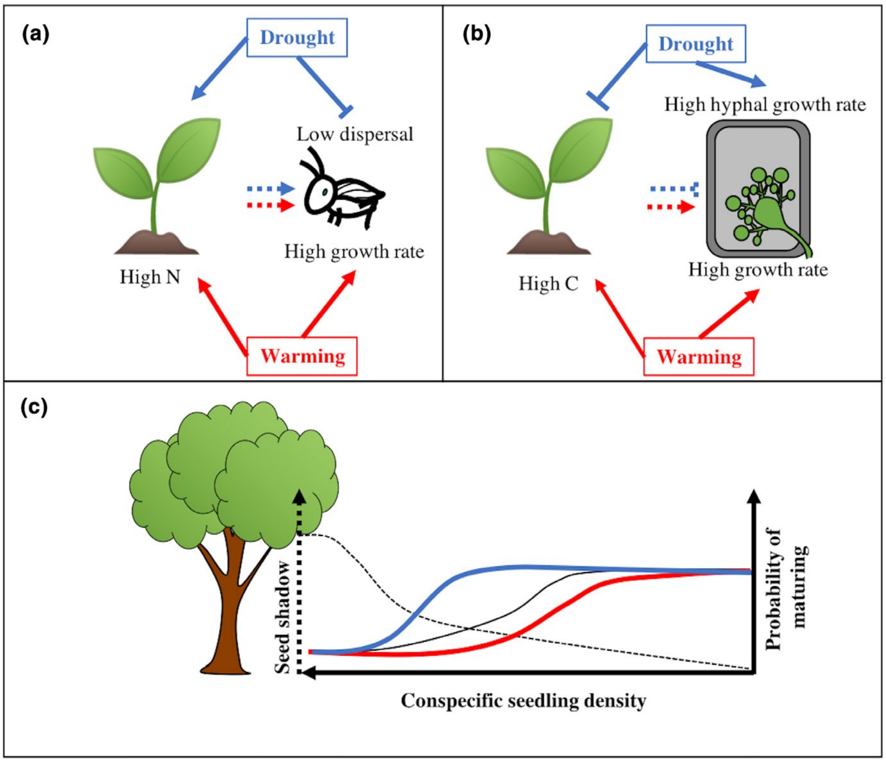

FIGURE 1 Conceptual diagrams showing hypothesized effects of climate on natural enemies (a), mycorrhizal fungi (b), and plant density dependence (c). In (a) and (b) positive effects are represented by lines ending in arrowheads, whereas negative effects are indicated by lines ending in a perpendicular line. Plain lines represent direct effects and dotted lines indicate indirect effects. Red lines represent hypotheses related to the experimental warming treatment and blue lines represent hypotheses related to drought. We hypothesized strong positive effects of warming on natural enemies due to direct and indirect effects and strong negative effects of drought on natural enemies due to direct effects (a). We hypothesized that direct effects of warming and drought on arbuscular mycorrhizal (AM) fungi would enhance AM fungal growth (b). In (c) we hypothesized that warming (red) and drought (blue) would increase and decrease negative density dependence resulting in lower and higher probability of a seedling maturing (right *y*-axis) compared to under unaltered climate conditions (black), respectively. Conspecific seedling density (*x*-axis) decreases with the seed shadow (left *y*-axis) away from the parent tree

little information on how temperature influences AM fungi in tropical forests; a climate change experiment in a temperate grassland found that experimental warming significantly increased AM fungi hyphal length and percent root colonization (Rillig, Wright, Shaw, & Field, 2002), both of which are linked with enhanced plant growth (Staddon & Fitter, 1998; Figure 1b). As such, there is the potential for increased temperature to drive positive density dependence via the positive effects of temperature on AM fungi in plants. Depending on the balance between these positive and negative effects on natural enemies and AM fungi, warming might lead to an increase in negative density dependence, a decrease in negative density dependence, or no change.

The effects of altered precipitation on plant density dependence might differ from that of temperature. For example, some plant natural enemies might prefer a high moisture environment (Chown & Terblanche, 2006; Coley, 1998; Wolda, 1978). Thus, increases in the frequency and severity of drought might directly reduce natural enemy abundance and richness, thereby reducing plant damage and negative density dependence (Figure 1a,c). Alternatively, plants might undergo stress during drought events. Under water stress, plant carbon allocation shifts away from carbon-rich compounds used for physical and chemical defense in leaves and toward belowground allocation to roots, resulting in higher concentrations of nitrogen in leaves (White, 1969). Plants with high nutrient content and low chemical defense are preferable to herbivores, and thus drought could also indirectly increase rates of herbivory, thereby increasing negative density dependence (Figure 1a). Simultaneously, with more carbon allocation belowground, drought could promote AM fungi in plants, which could in turn support positive density dependence by improving drought resistance in plants (Augé, 2001; Compant, Van Der Heijden, & Sessitsch, 2010). Field studies along precipitation gradients suggest that AM fungal community composition changes with decreasing precipitation (Deveautour, Donn, Power, Bennett, & Powell, 2018; Hawkes et al., 2011). Furthermore, mycorrhizal fungal abundance and richness have been found to increase during drought (Hawkes et al., 2011), but not always (Deveautour et al., 2018). Once again, it is the balance between the positive and negative density effects that will dictate how drought influences plant density dependence.

As a whole, predicting the net effects of climate on plant density dependence is challenging because each natural enemy, host plant, natural enemy predator, and mutualist might respond differently to altered temperature and moisture (van der Putten et al., 2010). In this way, the evaluation of naturally occurring extreme events and the use of in situ field experiments are invaluable tools for providing insight into how future climate might affect density-dependent controls on species diversity. Here, we took advantage of an extreme drought event as well as the first field warming experiment to be implemented in a tropical forested ecosystem (Tropical Responses to Altered Climate Experiment [TRACE]) to ask the following questions:

1. How do drought and warming influence negative density-dependent growth and mortality?
2. Are aboveground natural enemies and AM fungi responsible for changes in the strength of negative density-dependent feedbacks during the drought and in situ warming?

We hypothesized that the strength of negative density-dependent effects on seedling growth and mortality would decrease during drought and increase under warming conditions (Figure 1c). Furthermore, we hypothesized that observed changes would be driven by a decrease in natural enemy richness and abundance during drought conditions, but an increase in natural enemy richness and abundance under warming. Alternatively, an increase in associations with AM fungi under either warming or drought conditions could counteract the increase in natural enemy richness and abundance and promote positive density-dependent feedbacks. To limit damage to the experimental plots, we investigated AM fungal root colonization on the most common species, *Guarea guidonia*, collected near the plots. We focused specifically on seedling demographics because (a) seedlings are very sensitive to biotic interactions; and (b) the seedling stage is a key bottleneck in tree life history. To our knowledge, this is the first study to investigate how density-dependent feedbacks change during both an extreme drought event and in situ warming field experiment. Therefore, this study provides novel insights into how climate influences the biotic controls of tree diversity in a tropical forest.

2 | MATERIALS AND METHODS

2.1 | Study site

The study took place in a wet tropical forest (Holdridge, 1967) near the USDA Forest Service Sabana Field Research Station in the Luquillo Experimental Forest in Puerto Rico (LEF; 18°18′N, 65°50′W). The site was a 70-year-old secondary forest regenerating from agricultural land at the time of this study. The dominant canopy tree species are *Syzgium jambos*, *Ocotea leucoxylon*, and *Caseria arborea* and the palm *Prestoea montana*. In 2016, tree species richness was 50 species in 0.7 acre and stem (>1 cm) density was 3,100 trees/ha. Mean annual temperature of the site is 24°C, and mean annual rainfall is ~3,500 mm (Garcia-Martino, 1996). The site is located at an elevation of 100 m above sea level and is characterized by slopes ranging from 15° to 26° (Kimball et al., 2018). Soils are Ultisols (Scatena, 1989).

2.2 | Warming experiment

This study was conducted as part of the TRACE (Kimball et al., 2018). The experiment consists of six 4-m diameter hexagonal plots. Three plots are warmed at +4°C relative to the three control plots (see Kimball et al., 2018 for full experiment description). Warming occurs 24 hr/day using infrared heaters (Model Raymax 1010; Watlow

Electric Manufacturing Co.) and as measured with infrared thermometers (Model SI-121; Apogee Instruments). A datalogger plus multiplexor (Model CR-1000 logger with Loggernet software and Model AM16/32 multiplexor; Campbell Scientific) contained the program to calculate the AV voltage (0–10 V) sent to the heaters in order to maintain 4°C difference between control and warmed plots (Kimball et al., 2018). Each plot is separated into four quadrats (3 m^2 each). In this study, quadrat was the scale used to define the neighborhood of each seedling.

2.3 | Seedling survey

In June 2015, every woody seedling of at least 10 cm height in the plots was tagged, measured (height and root collar diameter), and identified to the species level. Puerto Rico experienced a historic drought during this summer (April–August 2015), which corresponded to an El Niño Southern Oscillation event. During this event, the Luquillo Experiment Forest experienced a reduction in total annual precipitation of 48% compared to total annual precipitation for the previous decade, and a drop of 14% in soil moisture (O'Connell, Ruan, & Silver, 2018). We also surveyed the seedlings in Fall 2015 following the drought event to capture initial post-drought responses. Seedlings were surveyed again in June 2016, providing a census in the absence of drought, but prior to warming. In Fall 2016, the warming began, and we surveyed the seedlings in June 2017 to observe initial responses to warming. Therefore, all seedlings tagged in 2015 experienced a drought event, surviving and recruiting seedlings experienced a normal precipitation year in 2016, and a portion of the surviving and recruiting seedlings (those in the warmed plots) experienced a warming treatment the following year. In this study, we include all individuals whose height was less than 2 m.

2.4 | Aboveground natural enemy survey

During each seedling census, we recorded the total amount of foliar damage observed for each seedling. The amount of foliar damage was assessed using percent of leaf damage and recorded as a categorical variable (ranging from 0% to 100% by 5% increments). Additionally, following a previous study (Bachelot & Kobe, 2013), we took pictures of up to five leaves of each seedling present in half of each 12 m^2 plot. Pictures were processed to identify damage morphotypes. The number of unique damage morphotypes (i.e., damage morphotype richness) was then used as a proxy for aboveground natural enemy richness (Bachelot & Kobe, 2013). We were also interested in the guilds of natural enemies. Therefore, unique damage morphotypes were classified as belonging to five groups: Gall makers, grazers, endophytes, leaf miners, and pathogens. Within each of these groups, we calculated the number of unique damage morphotypes and used this number as a proxy for aboveground natural enemy richness for a given group.

2.5 | Mycorrhizal root colonization outside treatment plots

In June 2017, to investigate mycorrhizal root colonization, we sampled 48 seedlings total, eight seedlings each at 2 and 4 m outside of each plot. We expected to detect changes in root morphology and mycorrhizal root colonization, if the seedlings outside the warming plots responded to changes in edaphic and biotic factors inside the treatment plots. Such responses could be because of residual warming and/or a decrease in moisture outside the treatment plots (Kimball et al., 2018), or if seedlings are able to sense and respond to changes happening inside the treatment plots. Seedlings were placed in transparent and sterile bags, brought back to the laboratory, and scanned using WinRHIZO (Regent Instruments Inc.). WinRHIZO enabled us to analyze root morphology (length, volume, area, and number of tips per diameter class). Seedlings were then kept frozen in a −80°C freezer until being shipped overnight to North Dakota State University. There, we assessed AM root colonization using the trypan blue staining method (Phillips & Hayman, 1970). After staining, samples were mounted in polyvinyl-lactoglycerol on microscope slides and scored at 200× magnification using a modified gridline intersect method (McGonigle, Miller, Evans, Fairchild, & Swan, 1990) on a Zeiss Axioscope A1 with differential interference contrast (Carl Zeiss AG). Because seedling root systems varied in size, the number of intersections scored was proportional to the size of the sample.

2.6 | Statistical analyses

To investigate how seedling demographics changed due to major climatic disturbances (drought and warming), we fitted Bayesian individual growth and mortality models. Both growth ($g_{i,s,t}$) and mortality of an individual seedling i from species s under the treatment t (control, drought, and warming) were fitted as functions of treatment-specific intercepts (μ_t), seedling height (HEIGHT_i), conspecific seedling density (CONS_i), heterospecific seedling density (HET_i), and the amount of foliar damage (DAM_i). We allowed the effects of height, conspecific and heterospecific seedling densities, and foliar damage to change with treatment ($\beta_{i,t}$). Finally, each model included species (σ_{species}), plot (σ_{plot}), and individual seedling (σ_{stem}) random effects to account for repeated measurements. The seedling growth and mortality models took the following form:

$$g_{i,s,t} \sim N(\mu_t + \beta_{1,t}\text{HEIGHT}_i + \beta_{2,t}\text{CONS}_i + \beta_{3,t}\text{HET}_i + \beta_{4,t}\text{DAM}_i + \sigma_{\text{species}} + \sigma_{\text{plot}} + \sigma_{\text{stem}}, \sigma),$$

$$m_{i,s,t} \sim B\left(\text{logistic}^{-1}(\mu_t + \beta_{1,t}\text{HEIGHT}_i + \beta_{2,t}\text{CONS}_i + \beta_{3,t}\text{HET}_i + \beta_{4,t}\text{DAM}_i + \sigma_{\text{plot}} + \sigma_{\text{stem}})^{\text{time}}\right).$$

To evaluate whether the main effects of conspecific density differed across treatment, we used pairwise Kolmogorov–Smirnov tests. This method compares whether two independent samples arise from the same distribution and is therefore well adapted to compare posterior distributions. We used non-informative priors for each variable, and we ran three Markov Chains with 10,000 iterations. Significance for each parameter was assessed by non-overlap of the 95% credible intervals (CIs) with 0. We assessed convergence, using $\hat{R}$ (Brook & Gelman, 1997). Goodness of fit was evaluated using Bayesian *p* value of the average mortality and growth rate (Gelman et al., 2013) and posterior predictive checks.

To investigate changes in aboveground natural enemy pressure and AM fungi root colonization, we used mixed linear models. We fitted a linear model of foliar damage and natural enemy richness using seedling height and treatment as fixed effects. Plot, species, and individual ID were used as random effects. Differences in richness of aboveground natural enemy guilds were assessed using Student's *t* test between treatments. AM root colonization was expressed as a function of seedling height, treatment, and distance from plot (2 or 4 m), and plot was used as a random effect.

All the covariates were log-transformed to correct for skewedness and *z*-transformed across individuals to allow for comparison of their effect size (Gelman et al., 2013). Seedling height was *z*-transformed within species to correct for different size distributions and improve convergence (Brook & Gelman, 1997). The amount of foliar damage was square-root transformed then scaled. Analyses were performed using R statistical software (R Core Team, 2017) and rstan package (Stan Development Team, 2018).

3 | RESULTS

3.1 | Weak negative density-dependent growth

The growth model converged ($\hat{R} = 1$, Bayesian *p* = .4), but the majority of the variation in seedling growth remained unexplained (R^2 = 7%, CI 6%–8%). Increasing conspecific density was significantly associated with decreasing seedling growth in warming plots (mean posterior distribution −0.11, CI −0.22 to −0.002; Figure 2a). In addition, in control plots, increased heterospecific seedling density was also strongly correlated with decreased seedling growth (−0.22 with CI −0.29 to −0.14; Figure 2a). Notably, during the drought event, seedling growth was not negatively correlated with conspecific or heterospecific seedling density (Figure 2a). Overall, negative density-dependent growth was weak and even dissipated during the drought event (Figure 3a). Finally, the amount of foliar damage by natural enemies was not a significant predictor of seedling growth (Figure 2a).

3.2 | Positive density-dependent mortality during in situ warming

The mortality model fitted the data well (Bayesian *p* = .6). As expected, in the control plots, seedling mortality was positively correlated with conspecific seedling density (Figure 2b). In contrast, during in situ warming and drought, the risk of mortality significantly decreased with the presence of conspecific seedlings (Figure 2b). Specifically, the presence of 25 conspecific individuals was associated with a 7% (CI 1%–11%) decrease in probability of mortality during in situ warming compared to when there were eight conspecific individuals. Heterospecific seedling density was only correlated with increasing mortality in the control plots (Figure 2b). Therefore, we only observed positive density-dependent mortality during warming and lack of negative density dependence during drought events (Figure 3b). Foliar damage significantly increased with seedling mortality risk during in situ warming and the drought event (Figure 2b).

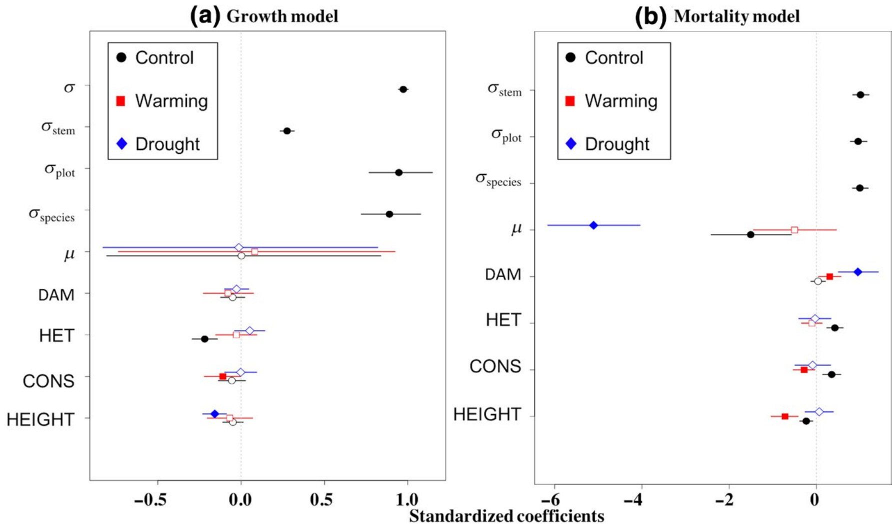

FIGURE 2 Standardized coefficients of the parameters in the growth (a) and mortality (b) models. Open symbols show non-significant effects (credible intervals [CIs] overlap with 0), whereas filled symbols indicate significant effects. Lines expand to the 95% CIs. The main covariates are seedling height (HEIGHT), conspecific seedling density (CONS), heterospecific seedling density (HET), and amount of foliar damage (DAM). The symbol μ represents treatment-specific intercept, and the symbols $\sigma_{species}$, σ_{plot} and σ_{stem} are species, plot and individual random effects, respectively. Finally, in the growth model, σ represents the error associated with the growth model

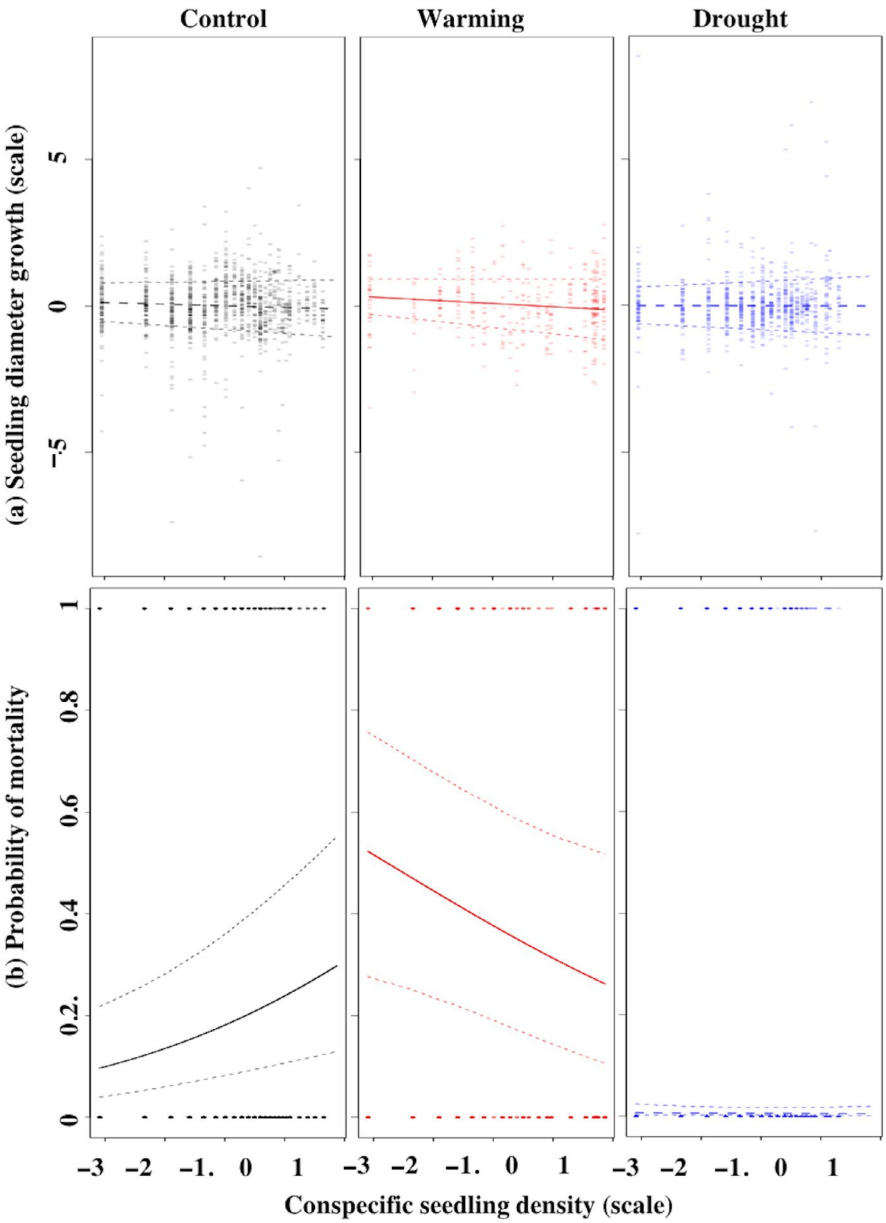

FIGURE 3 Seedling diameter growth (a) and probability of mortality (b) as a function of conspecific seedling density for control, drought, and in situ warming treatments. Thin dashed lines represent the 95% credible intervals, and thick lines show the mean posterior. The relationships between diameter growth during the drought and conspecific seedling density and between probability of mortality in control plots and conspecific seedling density are not significant

3.3 | Increase in enemy pressure during drought events and in situ warming

The amount of foliar damage significantly increased during the drought event and the richness of natural enemies targeting seedlings tended to increase with in situ warming, although this relationship was not significant (Figure 4). There were strong differences across species; some species, such as *O. leucoxylon*, experienced high pressure from aboveground natural enemies during extreme climate (drought and warming), whereas other species, such as *Roystonea boriquena*, suffered less from aboveground natural enemies (Figure S1). The richness of endophytes and leaf miners was significantly higher during the drought event than during the following year (Figure 5). In contrast, the richness of grazers was lower during the drought compared to the following year (Figure 5). The richness of grazers increased during in situ warming (Figure 5). Finally, pathogen richness was consistently lower during the more extreme climate of drought and warming (Figure 5).

3.4 | Changes in root architecture and AM fungal percent root colonization of *G. guidonia* around warming plots

Root morphology was significantly different in the seedlings collected near the warming plots compared to near the control plots. More specifically, there were more fine roots at 2 m away from the warming plots than from 2 m away from the control plots (Figure S2). This result was, however, only marginally significant when including seedlings from 4 m away from the plot. We found no significant differences in AM fungal percent root colonization of *G. guidonia* among the samples collected near the control or warming plots.

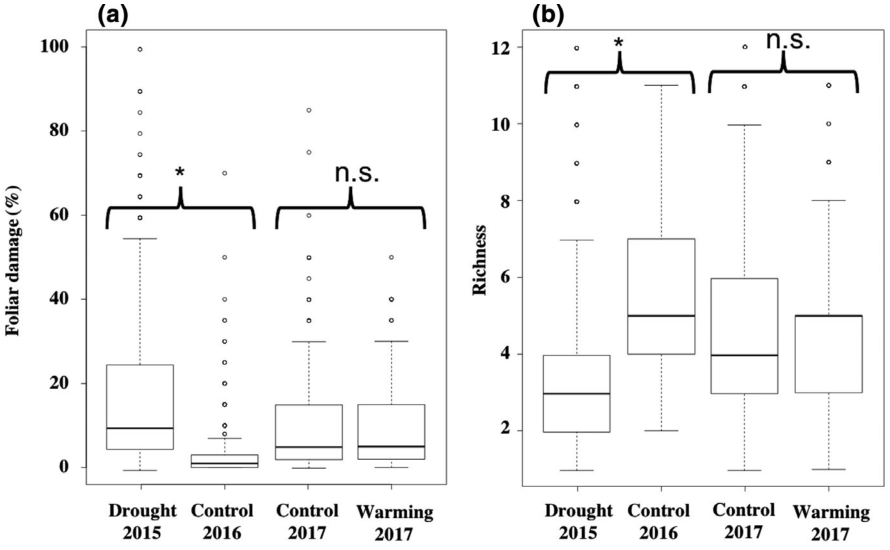

FIGURE 4 Changes in natural enemy pressure experienced by seedlings across the three treatments. We distinguished control treatment in 2016 (post-drought) and in 2017 to account for potential annual fluctuations. We used two measures of natural enemy pressure: amount of foliar damage (a) and damage morphotype richness (b). Asterisks indicate significant differences ($p < .05$), whereas n.s. signifies no significant differences among treatments

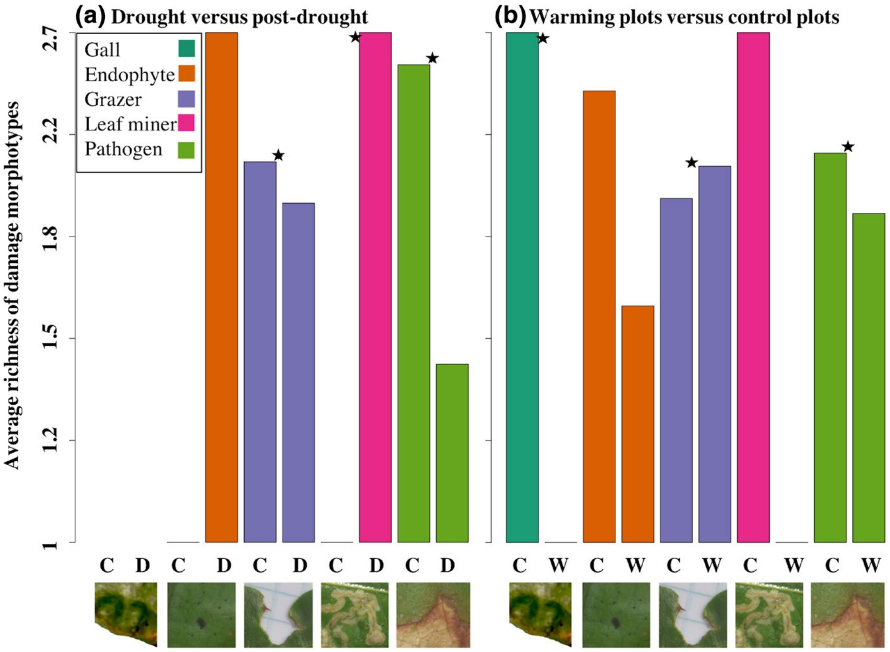

FIGURE 5 Changes in natural enemy composition following drought (a) and during the warming treatment (b). C indicates control plot and D and W stand for drought and in situ warming, respectively. Stars indicate significant differences in average richness (*t* tests) in guild between drought and control in (a) or between control and warming in (b)

4 | DISCUSSION

To our knowledge, this is the first study that combines observation and experimentation to investigate how density-dependent feedbacks change during in situ warming and drought. In light of previous observational studies, we hypothesized that negative density dependence should become stronger during warming and weaker during drought (Bachelot et al., 2015; Comita et al., 2014; Figure 1c). Contrary to our expectation, we found that seedling mortality transitioned to suggest positive density-dependent effects (i.e., less mortality under greater conspecific density) during in situ warming and a lack of negative density-dependent effects during the drought. If these patterns held across long timescales, such responses to warming and drought could have dramatic consequences for tree species coexistence in species-rich tropical forests (Figure 6). It is important to acknowledge that our experiment represents an abrupt change in temperature rather than a gradual increase to +4°C. This more 'extreme' warming rate might help explain the differences from previous work (Bachelot et al., 2015; Comita et al., 2014) and future studies should investigate how warming magnitude and rate influence negative density dependence.

The observed 'release' of negative density-dependent controls was not driven by a decrease in aboveground natural enemy pressure, as aboveground natural enemy damage and richness tended to increase during the drought and in situ warming, respectively (Figure 6). Therefore, results suggest that acquisition of resources and the belowground biota (enemies and AM fungi) may be affected. Consistent with this idea, we found more fine roots in *G. guidonia* near the warming plots compared to the control plots (Figure 6). However, the quality of the data did not allow us to test for changes in mycorrhizal fungal root colonization. Our understanding could benefit greatly from future studies, such as those using use greenhouse experiments, that can

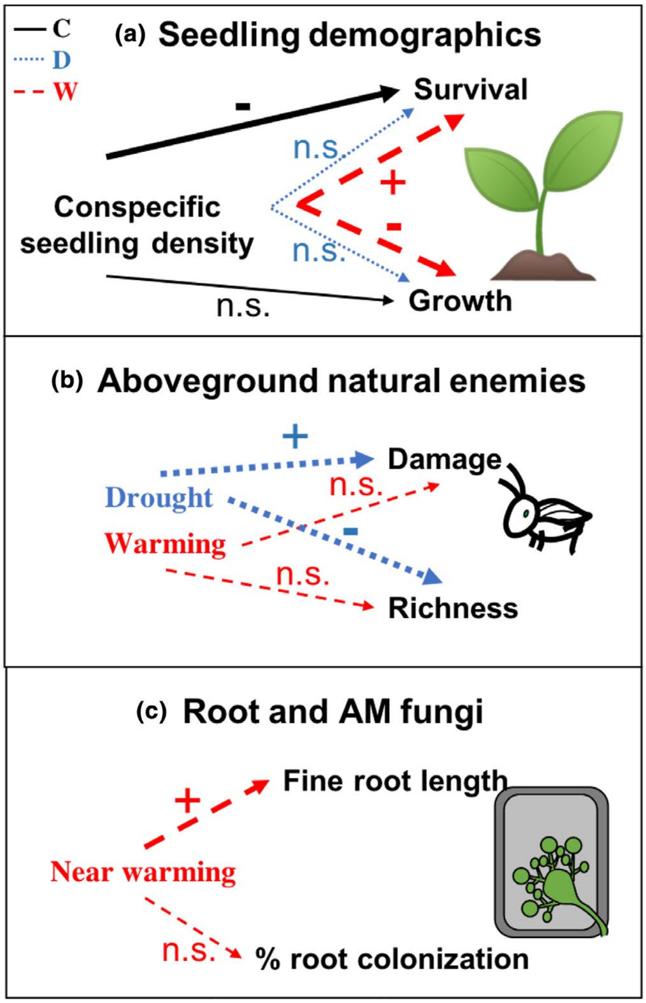

FIGURE 6 Conceptual figure summarizing the results about seedling demographics (a), aboveground natural enemies (b), root and arbuscular mycorrhizal (AM) fungi (c). Black arrows represent the effect in control plots, blue dotted arrows show the effects of drought, and dashed red arrows stand for the effect of in situ warming. Direction of the association is indicated with a positive or negative sign or n.s. for non-significant associations

more fully disentangle the abiotic and biotic mechanisms behind the observed positive density-dependent feedbacks.

4.1 | Weak negative density-dependent effects on seedling growth

Surprisingly, we detected negative density-dependent feedbacks on seedling growth only in the warmed plots (Figure 6). This result could in part be driven by an increase in enemy richness in the warming relative to control plots. Defense against several enemies can be costlier than defense against few enemies (Poitrineau, Brown, & Hochberg, 2003), resulting in higher allocation of resources toward defense instead of growth. Therefore, an increase in natural enemy richness might help explain negative density dependence in the warming plots.

In contrast, in the control plots, we found significant negative effects of heterospecific seedling density but no conspecific negative density-dependent growth. These results suggest weak negative density-dependent growth in this forest because seedling growth was more strongly constrained by heterospecific than by conspecific individuals. This finding is unexpected because negative density dependence tends to be pervasive in tropical rainforests (Clark & Clark, 1984; Comita et al., 2014). However, these studies usually test negative density dependence on seedling mortality (e.g., Bachelot et al., 2015). Seedling growth patterns can be very noisy and depend strongly on abiotic factors such as light availability (Kobe, 1999). Consistent with this idea, our growth model explained little growth variation.

The lack of strong negative density-dependent growth could be the result of the intense drought of summer 2015. During the drought event, seedlings grew faster and survived more than during the other censuses. This increase in seedling fitness might be due to a lagged effect of drought (Berdanier & Clark, 2016; Peltier, Fell, & Ogle, 2016). Studies on tree responses to drought have highlighted increased tree mortality in the years following the drought, suggesting a lag effect of water stress (Berdanier & Clark, 2016). However, a long-term study of seedling dynamics in the El Verde Long-Term Ecological Research site (Luquillo, Puerto Rico) found strong negative density-dependent effects during the rainy years and at dry sites (Uriarte, Muscarella, & Zimmerman, 2018), suggesting an immediate effect of rainfall regime on seedlings. Alternatively, we might have only surveyed surviving seedlings in 2015, possibly because they performed well at high conspecific seedling densities. Unfortunately, we have no data prior to the drought to test for these drought effects through time.

4.2 | Positive density-dependent mortality during in situ warming

Contrary to our hypothesis, we found that negative density-dependent mortality was weaker during extreme climate (drought and warming) than in the control plots (Figure 6). More surprising was the fact that we observed positive density-dependent mortality for the warming treatment. Negative density dependence arises from the sum of negative and positive effects (Liang et al., 2015). Positive density dependence suggests that either the positive effects are strong and/or the negative effects are weak during in situ warming.

The stress gradient hypothesis (SGH; Bertness & Callaway, 1995) predicts that interspecific species interactions should shift from negative (competitive) to positive (facilitative) with environmental stress. Most SGH studies focus on arid systems, but a few studies found evidence of facilitation under stress in tropical rainforests (Ganade & Brown, 2002; Gómez-Aparicio, 2009; Rigg, Enright, Perry, & Miller, 2002; Vieira, Uhl, & Nepstad, 1994). With the accumulation of SGH studies, refinements have been made to account for life history, type of stressors, ontogeny, and temporal variations (Butterfield, Bradford, Armas, Prieto, & Pugnaire, 2016; Maestre, Callaway, Valladares, & Lortie, 2009; Miriti, 2006).

Studies have also started to apply the SGH to intraspecific interactions and found similar shifts toward positive density dependence under stress in alpine clonal grasses (Chu et al., 2008), intertidal plants (Goldenheim, Irving, & Bertness, 2008), and seedlings in forest–grassland ecotones (Fajardo & McIntire, 2011). Therefore, our study supports intraspecific SGH in tropical rainforests with warming and drought as stressors. The mechanisms behind the SGH are poorly understood and rarely investigated (Michalet & Pugnaire, 2016) but could consist in habitat amelioration (Butterfield et al., 2016), defense against enemies (Lortie, Filazzola, & Sotomayor, 2016), and association with microorganisms (Rodríguez-Echeverría, Lozano, & Bardgett, 2016; van der Heijden & Horton, 2009). In this context, the results presented here represent some of the first work to assess how and why tropical seedlings will respond to predicted future climate.

We hypothesized that natural enemy pressure might increase in the warming plots due to increased natural enemy growth rate (Bale et al., 2002), increased nitrogen in plant tissue (Coley, 1998), or increased plant stress (Roy, Güsewell, & Harte, 2004; White, 1969; Figure 1a). In contrast, we hypothesized a decrease in natural enemy pressure during the drought event because low moisture can reduce the spread of pathogens (Desprez-Loustau, Marçais, Nageleisen, Piou, & Vannini, 2006; Figure 1a). We found that, overall, the amount of foliar damage increased during the drought event and the richness of natural enemies tended to increase with in situ warming (Figure 6). In particular, the richness of grazers significantly increased with in situ warming (Figure 5). Temperature and moisture can directly influence natural enemy populations by influencing natural enemy growth rate and spread, and indirectly alter their populations by changing plant fitness, tissue quality, or their predator communities (van der Putten et al., 2010).

Many studies have highlighted that these climatic effects are guild- and species-specific (Gutbrodt, Mody, & Dorn, 2011; Huberty & Denno, 2004). Using damage morphotypes to assign natural enemy guilds, we found that leaf miner richness increased during drought, whereas grazer richness and pathogen richness decreased. In contrast, grazer richness increased in the warming plots, whereas pathogen richness decreased. Few studies have investigated how different guilds of natural enemies responded to altered climate (Huberty & Denno, 2004). Ultimately, our results suggest that positive density-dependent mortality for the warming treatment was not due to a decrease in overall aboveground natural enemy pressure. However, the decrease in pathogen richness during the drought and in situ warming could be responsible for the lack of negative density-dependent mortality. Previous studies highlighted the key role played by fungal pathogens in inducing negative density dependence (Augspurger, 1984; Bagchi et al., 2010). Fungal pathogens are likely sensitive to changes in rainfall regime and the decreases in moisture induced by in situ warming (Swinfield, Lewis, Bagchi, & Freckleton, 2012). Additionally, belowground natural enemy communities might have changed in response to drought and warming. For example, elevated CO_2 was associated with increased abundance of belowground larvae of clover root weevil (Johnson & McNicol, 2010). Future studies investigating changes in belowground natural enemy pressure during drought events and in situ warming in tropical wet forests could be highly valuable.

Soil microorganisms could also be responsible for facilitation and positive density dependence by mitigating or exacerbating the effects of stressful environments (David, Thapa-Magar, & Afkhami, 2018). This mitigation-exacerbation continuum framework (David et al., 2018) was proposed as an extension of the SGH in light of recent empirical evidence highlighting the role of soil microorganisms in facilitation (Montesinos-Navarro, Segarra-Moragues, Valiente-Banuet, & Verdú, 2012; Montesinos-Navarro, Valiente-Banuet, & Verdú, 2018; Rodríguez-Echeverría, Armas, Pistón, Hortal, & Pugnaire, 2013; Rodríguez-Echeverría et al., 2016; van der Heijden & Horton, 2009; van der Putten, 2009). In particular, mycorrhizal fungi have been shown to promote interspecific facilitation in stressful environments (Montesinos-Navarro et al., 2012, 2018; van der Heijden & Horton, 2009). Therefore, we argue that the observed positive density dependence might also be due to changes in mutualist communities.

Root architecture of *G. guidonia* seedlings showed significant differences when collected near the warming versus near the control plots. In particular, fine root length was significantly higher near warming plots (Figure 6). The effects of warming on root architecture and AM fungal communities have been investigated in grassland ecosystems (Hawkes, Hartley, Ineson, & Fitter, 2008; Kim et al., 2015; Rillig et al., 2002). These studies do not always find a significant effect of warming on root architecture (Rillig et al., 2002). However, when non-tropical studies detect significant root changes, their results agree with our observation of increased fine root length (Majdi & Öhrvik, 2004; Wan, Norby, Pregitzer, Ledford, & O'Neill, 2004). Such changes in fine root length likely arise from changes in plant carbon allocation (Bai, Xia, Wan, Zhang, & Li, 2012). Increased temperature might enhance decomposition, resulting in nutrient pulses (Hopkins, Torn, & Trumbore, 2012). Investing in more belowground biomass enables the plants to directly compete for these nutrient pulses or indirectly via AM fungi. Alternatively, warming caused more variable soil moisture, including stronger dry-down periods (Kimball et al., 2018). As a result, the plants might need to invest more belowground directly (fine roots) and indirectly (AM fungi) to access water. Consistent with this idea, many grassland studies have found greater AM fungal hyphal length and percent root colonization in warming compared to ambient conditions (Hawkes et al., 2008; Kim et al., 2015; Rillig et al., 2002). However, we found no significant differences in percent root colonization among the samples collected near the control and warming plots (Figure 6). This lack of a difference could be in part explained by the low number and quality of the root samples, or the fact that samples taken just outside the plots did not experience enough of a treatment effect for responses to be detected. Future studies that investigate this pattern across several tree species and that can also elucidate AM fungal community composition could greatly help our understanding of how tropical rain forest AM fungi and their function change under altered climate regimes.

This study is the first field study of the effects of warming and drought on tropical wet forest understory seedling growth and survival and therefore provides unique insight into how seedling communities will respond to altered climate. Negative density dependence is an important mechanism regulating seedling dynamics in tropical wet forests. Our results show that altered climate likely influences seedling dynamics by decreasing negative density dependence and enhancing positive density dependence for seedling mortality. Positive density-dependent mortality might, in part, be due to decreased pathogen pressure and changes in AM fungal community composition. Such positive density-dependent feedbacks on seedling survival might have dramatic effects on tropical wet forest tree composition if these effects are permanent. Future studies assessing the long-term effects of altered climate on seedling dynamics and tropical wet forest composition could greatly improve our understanding of how these diverse systems are and will continue to respond to climatic change.

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DATA AVAILABILITY STATEMENT

Data will be made available on the USDA FS data archive upon publication.

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REFERENCES

Augé, R. M. (2001). Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. *Mycorrhiza*, *11*, 3–42. https://doi.org/10.1007/s005720100097

Augspurger, C. K. (1984). Seedling survival of tropical tree species: Interactions of dispersal distance, light-gaps, and pathogens. *Ecology*, *65*, 1705–1712. https://doi.org/10.2307/1937766

Bachelot, B., & Kobe, R. K. (2013). Rare species advantage? Richness of damage types due to natural enemies increases with species abundance in a wet tropical forest. *Journal of Ecology*, *101*, 846–856. https://doi.org/10.1111/1365-2745.12094

Bachelot, B., Kobe, R. K., & Vriesendorp, C. (2015). Negative density-dependent mortality varies over time in a wet tropical forest, advantaging rare species, common species, or no species. *Oecologia*, *179*, 853–861. https://doi.org/10.1007/s00442-015-3402-7

Bachelot, B., Uriarte, M., McGuire, K. L., Thompson, J., & Zimmerman, J. (2017). Arbuscular mycorrhizal fungal diversity and natural enemies promote coexistence of tropical tree species. *Ecology*, *98*, 712–720. https://doi.org/10.1002/ecy.1683

Bagchi, R., Swinfield, T., Gallery, R. E., Lewis, O. T., Gripenberg, S., Narayan, L., & Freckleton, R. P. (2010). Testing the Janzen–Connell mechanism: Pathogens cause overcompensating density dependence in a tropical tree. *Ecology Letters*, *13*, 1262–1269. https://doi.org/10.1111/j.1461-0248.2010.01520.x

Bai, W. M., Xia, J. Y., Wan, S. Q., Zhang, W. H., & Li, L. H. (2012). Day and night warming have different effect on root lifespan. *Biogeosciences*, *9*, 375–384. https://doi.org/10.5194/bg-9-375-2012

Bale, J. S., Masters, G. J., Hodkinson, I. D., Awmack, C., Bezemer, T. M., Brown, V. K., … Whittaker, J. B. (2002). Herbivory in global climate change research: Direct effects of rising temperature on insect herbivores. *Global Change Biology*, *8*, 1–16. https://doi.org/10.1046/j.1365-2486.2002.00451.x

Berdanier, A. B., & Clark, J. S. (2016). Multiyear drought-induced morbidity preceding tree death in southeastern U.S. forests. *Ecological Applications*, *26*, 17–23. https://doi.org/10.1890/15-0274

Bertness, M. D., & Callaway, R. (1995). Positive interactions in communities. *Trends in Ecology & Evolution*, *9*, 191–193. https://doi.org/10.1016/0169-5347(94)90088-4

Brook, S. P., & Gelman, A. (1997). General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics*, *7*, 434–455. https://doi.org/10.1080/10618600.1998.10474787

Butterfield, B. J., Bradford, J. B., Armas, C., Prieto, I., & Pugnaire, F. I. (2016). Does the stress-gradient hypothesis hold water? Disentangling spatial and temporal variation in plant effects on soil moisture in dryland systems. *Functional Ecology*, *30*, 10–19. https://doi.org/10.1111/1365-2435.12592

Chown, S. L., & Terblanche, J. S. (2006). Physiological diversity in insects: Ecological and evolutionary contexts. *Advances in Insect Physiology*, *33*, 50–152. https://doi.org/10.1016/S0065-2806(06)33002-0

Chu, C.-J., Maestre, F. T., Xiao, S. A., Weiner, J., Wang, Y.-S., Duan, Z.-H., & Wang, G. (2008). Balance between facilitation and resource competition determines biomass – Density relationships in plant populations. *Ecology Letters*, *11*, 1189–1197. https://doi.org/10.1111/j.1461-0248.2008.01228.x

Clark, D. A., & Clark, D. B. (1984). Spacing dynamics of a tropical rain forest tree: Evaluation of the Janzen–Connell model. *American Naturalist*, *124*, 769–788. https://doi.org/10.1086/284316

Coley, P. D. (1998). Possible effects of climate change on plant/herbivore interactions in moist tropical forests. *Climate Change*, *39*, 455–472. https://doi.org/10.1023/A:1005307620024

Comita, L. S., Queenborough, S. A., Murphy, S. J., Eck, J. L., Xu, K., Krishnadas, M., … Zhu, Y. (2014). Testing predictions of the Janzen–Connell hypothesis: A meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. *Journal of Ecology*, *102*, 845–856. https://doi.org/10.1111/1365-2745.12232

Compant, S., Van Der Heijden, M. G. A., & Sessitsch, A. (2010). Climate change effects on beneficial plant–microorganism interactions. *FEMS Microbiology Ecology*, *73*, 197–214. https://doi.org/10.1111/j.1574-6941.2010.00900.x

Connell, J. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Dynamics of Populations*, *1971*, 298–312.

David, A. S., Thapa-Magar, K. B., & Afkhami, M. E. (2018). Microbial mitigation-exacerbation continumm: A novel framework for microbiome effects on hosts in the face of stress. *Ecology*, *99*, 517–523. https://doi.org/10.1002/ecy.2153

Desprez-Loustau, M.-L., Marçais, B., Nageleisen, L.-M., Piou, D., & Vannini, A. (2006). Interactive effects of drought and pathogens in forest trees. *Annals of Forest Science*, *63*, 597–612. https://doi.org/10.1051/forest:2006040

Deveautour, C., Donn, S., Power, S. A., Bennett, A. E., & Powell, J. R. (2018). Experimentally altered rainfall regimes and host root traits affect grassland arbuscular mycorrhizal fungal communities. *Molecular Ecology*, *27*, 2152–2163. https://doi.org/10.1111/mec.14536

Fajardo, A., & McIntire, E. J. B. (2011). Under strong niche overlap conspecifics do not compete but help each other to survive: Facilitation at the intraspecific level. *Journal of Ecology*, *99*, 642–650. https://doi.org/10.1111/j.1365-2745.2010.01771.x

Ganade, G., & Brown, V. (2002). Succession in old pastures of central Amazonia: Role of soil fertility and plant litter. *Ecology*, *83*, 743–754. https://doi.org/10.1890/0012-9658(2002)083[0743:SIOPOC]2.0.CO;2

Garcia-Martino, A. R., Warner, G. S., Scatena, F. N., & Civco, D. L. (1996). Rainfall, runoff and elevation relationships in the Luquillo Mountains of Puerto Rico. *Caribbean Journal of Science*, *32*, 413–424.

Gelman, A., Carlin, J., Stern, H., Dunson, D., Vehtari, A., & Rubin, D. (2013). *Bayesian data analysis*. Boca Raton, FL: Chapman and Hall/CRC.

Goldenheim, W. M., Irving, A. D., & Bertness, M. D. (2008). Switching from negative to positive density-dependence among populations of a cobble beach plant. *Oecologia*, *158*, 473–483. https://doi.org/10.1007/s00442-008-1157-0

Gómez-Aparicio, L. (2009). The role of plant interactions in the restoration of degraded ecosystems: A meta-analysis across life-forms and ecosystems. *Journal of Ecology*, *97*, 1202–1214. https://doi.org/10.1111/j.1365-2745.2009.01573.x

Gutbrodt, B., Mody, K., & Dorn, S. (2011). Drought changes plant chemistry and causes contrasting responses in lepidopteran herbivores. *Oikos*, *120*, 1732–1740. https://doi.org/10.1111/j.1600-0706.2011.19558.x

Hawkes, C. V., Hartley, I. P., Ineson, P., & Fitter, A. H. (2008). Soil temperature affects carbon allocation within arbuscular mycorrhizal networks and carbon transport from plant to fungus. *Global Change Biology*, *14*, 1181–1190. https://doi.org/10.1111/j.1365-2486.2007.01535.x

Hawkes, C. V., Kivlin, S. N., Rocca, J. D., Huguet, V., Thomsen, M. A., & Suttle, K. B. (2011). Fungal community responses to precipitation. *Global Change Biology*, *17*, 1637–1645. https://doi.org/10.1111/j.1365-2486.2010.02327.x

Holdridge, L. R. (1967). *Life zone ecology*. San Jose, Costa Rica: Tropical Science Center.

Hopkins, F. M., Torn, M. S., & Trumbore, S. E. (2012). Warming accelerates decomposition of decades-old carbon in forest soils. *Proceedings of the National Academy of Sciences of the United States of America*, *109*, E1753–E1761. https://doi.org/10.1073/pnas.1120603109

Huberty, A. F., & Denno, R. F. (2004). Plant water stress and its consequences for herbivorous insects: A new synthesis. *Ecology*, *85*, 1383–1398. https://doi.org/10.1890/03-0352

Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forests. *American Naturalist*, *104*, 501–528. https://doi.org/10.1086/282687

Johnson, S. N., & McNicol, J. W. (2010). Elevated CO_2 and aboveground-belowground herbivory by the clover root weevil. *Oecologia*, *162*, 209–216. https://doi.org/10.1007/s00442-009-1428-4

Karmalkar, A. V., Bradley, R. S., & Diaz, H. F. (2011). Climate change in Central America and Mexico: Regional climate model validation and climate change projections. *Climate Dynamics*, *37*, 605–629. https://doi.org/10.1007/s00382-011-1099-9

Kim, Y.-C., Gao, C., Zheng, Y., He, X.-H., Yang, W., Chen, L., … Guo, L.-D. (2015). Arbuscular mycorrhizal fungal community response to warming and nitrogen addition in a semiarid steppe ecosystem. *Mycorrhiza*, *25*, 267–276. https://doi.org/10.1007/s00572-014-0608-1

Kimball, B. A., Alonso-Rodríguez, A. M., Cavaleri, M. A., Reed, S. C., González, G., & Wood, T. E. (2018). Infrared heater system for warming tropical forest understory plants and soils. *Ecology and Evolution*, *8*, 1932–1944. https://doi.org/10.1002/ece3.3780

Kobe, R. K. (1999). Light gradient partitioning among tropical tree species through differential seedling mortality and growth. *Ecology*, *80*, 187–201. https://doi.org/10.1890/0012-9658(1999)080[0187:LGPATT]2.0.CO;2

Liang, M., Liu, X., Etienne, R. S., Huang, F., Wang, Y., & Yu, S. (2015). Arbuscular mycorrhizal fungi counteract the Janzen–Connell effect of soil pathogens. *Ecology*, *96*, 562–574. https://doi.org/10.1890/14-0871.1

Lortie, C. J., Filazzola, A., & Sotomayor, D. A. (2016). Functional assessment of animal interactions with shrub-facilitation complexes: A formal synthesis and conceptual framework. *Functional Ecology*, *30*, 41–51. https://doi.org/10.1111/1365-2435.12530

Lyra, A., Imbach, P., Rodriguez, D., Chou, S. C., Georgiou, S., & Garofolo, L. (2017). Projections of climate change impacts on central America tropical rainforest. *Climate Change*, *141*, 93–105. https://doi.org/10.1007/s10584-016-1790-2

Maestre, F. T., Callaway, R. M., Valladares, F., & Lortie, C. J. (2009). Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology*, *97*, 199–205. https://doi.org/10.1111/j.1365-2745.2008.01476.x

Majdi, H., & Öhrvik, J. (2004). Interactive effects of soil warming and fertilization on root production, mortality, and longevity in a Norway spruce stand in Northern Sweden. *Global Change Biology*, *20*, 182–188. https://doi.org/10.1111/j.1365-2486.2004.00733.x

McGonigle, T. P., Miller, M. H., Evans, D. G., Fairchild, G. L., & Swan, J. A. (1990). A new method which gives an objective measure of colonization of roots by vesicular—arbuscular mycorrhizal fungi. *New phytologist*, *115*, 495–501. https://doi.org/10.1111/j.1469-8137.1990.tb00476.x

Michalet, R., & Pugnaire, F. I. (2016). Facilitation in communities: Underlying mechanisms, community and ecosystem implications. *Functional Ecology*, *30*, 3–9. https://doi.org/10.1111/1365-2435.12602

Miriti, M. N. (2006). Ontogenetic shift from facilitation to competition in a desert shrub. *Journal of Ecology*, *94*, 973–979. https://doi.org/10.1111/j.1365-2745.2006.01138.x

Montesinos-Navarro, A., Segarra-Moragues, J. G., Valiente-Banuet, A., & Verdú, M. (2012). Plant facilitation occurs between species differing in their associated arbuscular mycorrhizal fungi. *New Phytologist*, *196*, 835–844. https://doi.org/10.1111/j.1469-8137.2012.04290.x

Montesinos-Navarro, A., Valiente-Banuet, A., & Verdú, M. (2018). Mycorrhizal symbiosis increases the benefits of plant facilitative interactions. *Ecography*, *41*, 1–9. https://doi.org/10.1111/ecog.03926

O'Connell, C. S., Ruan, L., & Silver, W. L. (2018). Drought drives rapid shifts in tropical rainforest soil biogeochemistry and greenhouse gas emissions. *Nature Communications*, *9*, 1348. https://doi.org/10.1038/s41467-018-03352-3

Peltier, D. M., Fell, M., & Ogle, K. (2016). Legacy effects of drought in the southwestern United States: A multiple-species synthesis. *Ecological Monograph*, *86*, 312–326. https://doi.org/10.1002/ecm.1219

Phillips, J. M., & Hayman, D. S. (1970). Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. *Transactions of the British Mycological Society*, *55*, 158–161. https://doi.org/10.1016/S0007-1536(70)80110-3

Poitrineau, K., Brown, S. P., & Hochberg, M. E. (2003). Defence against multiple enemies. *Journal of Evolutionary Biology*, *16*, 1319–1327. https://doi.org/10.1046/j.1420-9101.2003.00585.x

R Core Team. (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Rigg, L. S., Enright, N. J., Perry, G. L. W., & Miller, B. P. (2002). The role of cloud combing and shading by isolated trees in the succession from maquis to rain forest in New Caledonia. *Biotropica*, *34*, 199–210. https://doi.org/10.1111/j.1744-7429.2002.tb00531.x

Rillig, M. C., Wright, S. F., Shaw, M. R., & Field, C. B. (2002). Artificial climate warming positively in an water stability soil aggregate mycorrhizae but decreases annual grassland. *Oikos*, *97*, 52–58. https://doi.org/10.1034/j.1600-0706.2002.970105.x

Rodríguez-Echeverría, S., Armas, C., Pistón, N., Hortal, S., & Pugnaire, F. I. (2013). A role for below-ground biota in plant–plant facilitation. *Journal of Ecology*, *101*, 1420–1428. https://doi.org/10.1111/1365-2745.12159

Rodríguez-Echeverría, S., Lozano, Y. M., & Bardgett, R. D. (2016). Influence of soil microbiota in nurse plant systems. *Functional Ecology*, *30*, 30–40. https://doi.org/10.1111/1365-2435.12594

Roy, B. A., Güsewell, S., & Harte, J. (2004). Response of plant pathogens and herbivores to a warming experiment. *Ecology*, *85*, 2570–2581. https://doi.org/10.1890/03-0182

Scatena, F. N. (1989). *An introduction to the physiography and history of the Bisley Experimental Watersheds in the Luquillo Mountains of Puerto Rico*. General Technical Report SO-72. New Orleans, LA: US Department of Agriculture, Forest Service, Southern Forest Experiment Station, 22 pp. https://doi.org/10.2737/SO-GTR-72

Staddon, P. L., & Fitter, A. H. (1998). Does elevated atmospheric carbon dioxide affect arbuscular mycorrhizas? *Trends in Ecology & Evolution*, *13*, 455–458. https://doi.org/10.1016/S0169-5347(98)01493-1

Stan Development Team. (2018). *RStan: The R interface to Stan*. R package version 2.18.2. Retrieved from http://mc–stan.org/

Swinfield, T., Lewis, O. T., Bagchi, R., & Freckleton, R. P. (2012). Consequences of changing rainfall for fungal pathogen-induced mortality in tropical tree seedlings. *Ecology and Evolution*, *2*, 1408–1413. https://doi.org/10.1002/ece3.252

Uriarte, M., Muscarella, R., & Zimmerman, J. K. (2018). Environmental heterogeneity and biotic interactions mediate climate impacts on tropical forest regeneration. *Global Change Biology*, *24*, 692–704. https://doi.org/10.1111/gcb.14000

van der Heijden, M. G. A., & Horton, T. R. (2009). Socialism in soil? The importance of mycorrhizal fungal networks for facilitation in natural ecosystems. *Journal of Ecology*, *97*, 1139–1150. https://doi.org/10.1111/j.1365-2745.2009.01570.x

van der Heijden, M. G. A., Klironomos, J. N., Ursic, M., Moutoglis, P., Streitwolf-Engel, R., Boller, T., … Sanders, I. R. (1998). Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature*, *396*, 69–72. https://doi.org/10.1038/23932

van der Putten, W. H. (2009). Facilitation in plant communities: A multitrophic perspective on functioning and evolution of facilitation in plant communities. *Journal of Ecology*, *97*, 1131–1138. https://doi.org/10.1111/j.1365-2745.2009.01561.x

van der Putten, W. H., Macel, M., & Visser, M. E. (2010). Predicting species distribution and abundance responses to climate change: Why it is essential to include biotic interactions across trophic levels. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*, 2025–2034. https://doi.org/10.1098/rstb.2010.0037

Vieira, I. C. G., Uhl, C., & Nepstad, D. (1994). The role of the shrub *Cordia multispicata* Cham. as a 'succession facilitator' in an abandoned pasture, Paragominas, Amazônia. *Vegetatio*, *115*, 91–99. https://doi.org/10.1007/BF00044863

Wan, S., Norby, R. J., Pregitzer, K. S., Ledford, J., & O'Neill, E. G. (2004). CO_2 enrichment and warming of the atmosphere enhance both productivity and mortality of maple tree fine roots. *New Phytologist*, *162*, 437–446. https://doi.org/10.1111/j.1469-8137.2004.01034.x

White, T. C. R. (1969). An index to measure weather-induced stress of trees associated with outbreaks of psyllids in Australia. *Ecology*, *50*, 905–909. https://doi.org/10.2307/1933707

Wilf, P., & Labandeira, C. C. (1999). Response of plant-insect associations to Paleocene-Eocene warming. *Science*, *284*, 2153–2156. https://doi.org/10.1126/science.284.5423.2153

Wilson, E. O. (1992). *The diversity of life*. Cambridge, MA: Harvard University Press.

Wolda, H. (1978). Seasonal fluctuations in rainfall, food and abundance of tropical insects. *Journal of Animal Ecology*, *47*, 69–381. https://doi.org/10.2307/3789

Wright, S. J. (2010). The future of tropical forests. *Annals of the New York Academy of Sciences*, *1195*, 1–27. https://doi.org/10.1111/j.1749-6632.2010.05455.x

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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